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EVOLUTION, CYTOLOGY AND SUBGENERIC CLASSIFICATION IN *MORAEA* (IRIDACEAE)¹

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ABSTRACT

Moraea, an African genus widespread south of the Sahara, comprising ca. 92 species, is divided into five subgenera: *Moraea*, *Monocephalae*, *Visciramosa*, *Grandiflora*, and *Vieusseuxia*, and into several sections. Chromosome numbers of $n = 10, 9, 8, 6, 20,$ and 12 are reported in the 52 species studied to date. A base number of $x = 10$ is postulated for *Moraea*, and *Dietes* is suggested as the closest living ancestor. *Moraea* is pictured as having evolved in the mid to late Tertiary in central southern Africa in response to the onset of a dry climatic regime bordering the tropics. The great radiation of the genus in the southwestern Cape is seen as a more recent phenomenon resulting from the development of a Mediterranean climate in this area. Several nomenclatural changes are made and four new species are described.

The problem of infrageneric classification in *Moraea* was only briefly mentioned in my recent survey of the chromosome cytology of the southern African Iridaceae (Goldblatt, 1971a). In this work the karyotypes of several species were described and discussed with reference to the evolution of the genus, and although only a comparatively small number of species were studied, the cytological evidence was found to be at odds in many instances with existing subgeneric treatments. Thus it was clear that further cytological investigation would provide invaluable information for taxonomic and evolutionary studies and that it would be especially useful at infrageneric levels.

In preparation for a revision of the South African representatives of *Moraea*, which comprise the great majority of the species in the genus, I have undertaken a more extensive karyotypic study. Chromosomal data are now known for 52 species, approximately 70% of the genus, and this information has assisted considerably in evaluating the systematics of *Moraea* because of the strong correlations with certain morphological traits. The comparison of morphology and

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cytology has resulted in a complete rearrangement of the classification of Baker (1896), the most recent and only detailed treatment of the genus, and has made possible new interpretations of species relationships. The system presented here was first developed in a revision of the South African species in the summer rainfall area (Goldblatt, 1973), but was necessarily incomplete because of the limited occurrence of *Moraea* in this area. Moreover, no formal ranks between genus and species were recognized in this revision so that the subgeneric treatment is essentially new in the present work.

The cytological data are presented in the first section of the paper as these are central to the revised generic classification. The classification itself is then summarized, followed by an analysis of the karyology and by a phytogeographic and phylogenetic discussion. Finally, four new species are described and several necessary nomenclatural changes are explained.

CHROMOSOME CYTOLOGY

METHOD

The paraffin section method described earlier (Goldblatt, 1971a), was abandoned in favor of a rapid squash technique. Root tips from sprouting corms or germinating seeds were pretreated for three to four hours in 0.05% aqueous colchicine, fixed for two minutes in acetic ethanol 1:3, hydrolyzed in 10% HCl for five minutes at 60° C and squashed in lacto-propionic orcein (Dyer, 1963). This method yielded excellent preparations in the minimum time, and although slides could not readily be made permanent, they kept well for two to three days allowing adequate time for study.

OBSERVATIONS

The outstanding feature that emerges from the cytological survey of *Moraea* (Table 1) is the predominance of species with chromosome numbers based on either $x = 10$ ($2n = 20, 40$) and $x = 6$ ($2n = 12, 24, 36$); the few exceptions to this so far discovered are *M. papilionacea*, $2n = 18$, *M. fugax* in which $2n = 20, 16$ and 12 occur, and only one of the several populations of *M. ciliata* examined, also $2n = 18$ (Table 1). *Moraea papilionacea* is clearly allied to the group of species with $x = 10$ and must be regarded as an aneuploid species and not, as might appear, a triploid based on $x = 6$. The existence of a $2n = 18$ population in *M. ciliata* (predominantly $2n = 20$), requires more detailed study as its significance is not yet known, but as *M. ciliata* is also related to other species with $2n = 20$, the $2n = 18$ is clearly derived.

The situation in *M. fugax*, in which the three populations studied have quite different numbers, $n = 10, 8$ and 6 , is more complex. The immediate impression is that this species, if in fact it is only one species, is the link between the two main chromosome groups, which are based on $x = 10$ and $x = 6$. This interpretation does not seem correct simply on morphological grounds, since *M. fugax* has a very distinctive morphology which suggests it is not a direct ancestor of the large and heterogeneous group with $x = 6$.

TABLE 1. Chromosome numbers in *Moraea*. The following abbreviations are used: C.P. = Cape Province; Tvl. = Transvaal; S.W.A. = South West Africa.

Species	Diploid Chromosome Number	Collection Data or Reference to Previous Work
Subg. <i>MORAEA</i>		
Sect. <i>Moraea</i>		
<i>M. fergusoniae</i> L. Bol.	20	C.P.: Robinson Pass, <i>Heimstra s.n.</i> (MO). Botrivier-Villiersdorp, <i>Goldblatt 216</i> (BOL).
<i>M. gawleri</i> Spreng.	20	C.P.: Cape Point Res., (Goldblatt, 1971a).
<i>M. lugubris</i> (Salisb.) Goldbl.	24 20	C.P.: Van Rhyns Pass, <i>Goldblatt 223</i> (J).
<i>M. margaretae</i> Goldbl.	20	C.P.: Southern Cape Peninsula, <i>Goldblatt</i> , no voucher.
<i>M. papilionacea</i> (L.f.) Ker	40	C.P.: Near Nababeep, <i>Goldblatt 628</i> (BOL). Flats E of Nababeep, <i>Goldblatt 3061</i> (MO).
<i>M. ramosissima</i> (L.f.) Druce	18	C.P.: Tulbagh Road, (Goldblatt, 1971a). Constantia Nek, (Goldblatt, 1971a). Kenilworth flats, <i>Goldblatt</i> , no voucher.
<i>M. serpentina</i> Baker (or as <i>M. framesii</i> L. Bol.)	20	C.P.: Stellenbosch, (Goldblatt, 1971a) (Sakai, 1952).
<i>M. vegeta</i> L. (as <i>M. juncea</i>)	20	C.P.: Springbok, <i>Goldblatt 626</i> (BOL). Van Rhyns Pass, (Goldblatt, 1971a). Slopes W of Springbok, <i>Goldblatt 3043</i> (MO). 40 km S of Springbok, <i>Goldblatt 3041</i> (MO). C.P.: Groot Constantia, (Goldblatt, 1971a). (Fernandes & Neves, 1961).
Sect. <i>Deserticola</i>		
<i>M. bolusii</i> Baker	20	C.P.: Between Steinkopf and Okiep, <i>Goldblatt 2772</i> (MO).
Sect. <i>Acaules</i>		
<i>M. ciliata</i> (L.f.) Ker	20	C.P.: Nieuwoudtville, (Goldblatt, 1971a). Verlate Kloof, Sutherland, <i>Goldblatt 548</i> (BOL). Koedoes Mts., <i>Goldblatt</i> , no voucher.
	20, 18	C.P.: Glenlyon, Nieuwoudtville, <i>Strauss s.n.</i> (NBG 90218).
	18	C.P.: Darling-Mamre road, <i>Goldblatt</i> , no voucher.
	40	C.P.: Between Queen Anne and Eseljacht, <i>Goldblatt 2498</i> (MO).
<i>M. falcifolia</i> Klatt	20	C.P.: Nieuwoudtville, <i>Goldblatt 564</i> (BOL). 4 km W of Steinkopf, <i>Goldblatt</i> , no voucher.
<i>M. macronyx</i> Lewis	20	C.P.: Calvinia dist., (Goldblatt, 1971a). Near Avontuur, <i>Goldblatt 2860</i> (MO).
Sect. <i>Subracemosae</i>		
<i>M. fugax</i> (de la Roche) Jacq. (or as <i>M. edulis</i>)	12	C.P.: Hopefield, (Goldblatt, 1971a).
	16	C.P.: 10 km N of Malmesbury, <i>Goldblatt 3025</i> (MO).
	28	(Sakai, 1952).
<i>M. fugax</i> var. <i>gracilis</i> Baker	20	C.P.: Flats S of Pikenierskloof Pass, <i>Goldblatt 3279</i> (MO).
<i>M. filicaulis</i> Baker (as <i>M. diphylla</i> Baker)	12	C.P.: Giftberg, <i>Goldblatt 207</i> (BOL).

TABLE 1. (continued)

Species	Diploid Chromosome Number	Collection Data or Reference to Previous Work
Sect. <i>Tubiflora</i>		
<i>M. cooperi</i> Baker	20	C.P.: Caledon dist., (Goldblatt, 1971a).
Subg. <i>MONOCEPHALAE</i>		
<i>M. angusta</i> (Thunb.) Ker	20	C.P.: Malmesbury, (Goldblatt, 1971a).
<i>M. cf. angusta</i>	20	C.P.: Bainskloof, <i>Goldblatt</i> , no voucher.
<i>M. anomala</i> Lewis (as <i>M. neglecta</i>)	20	C.P.: Elim, (Goldblatt, 1971a).
<i>M. neglecta</i> Lewis	20	C.P.: Sandy flats E of Hermanus, <i>Goldblatt</i> 2999 (MO).
Subg. <i>VISCIRAMOSA</i>		
<i>M. bituminosa</i> (L.f.) Ker	20	C.P.: Hermanus, <i>Goldblatt</i> 3325 (MO).
<i>M. elsiae</i> Goldbl.	20	C.P.: Kenilworth Racecourse, <i>Esterhuysen</i> 32358 (BOL).
<i>M. odorata</i> Lewis	20	C.P.: Quoin Pt., (Goldblatt, 1971a). Rondebosch Common, <i>Barnard s.n.</i> (BOL).
<i>M. "viscaria"</i> (L.f.) Ker	20	C.P.: Giftberg, <i>Goldblatt</i> 353 (BOL). Near Elim, <i>Goldblatt</i> , no voucher.
Subg. <i>VIEUSSEUXIA</i>		
Sect. <i>Polyanthes</i>		
<i>M. carsonii</i> Baker	12	Zambia: Kandalila Falls, <i>Strid</i> 2900 (C).
<i>M. elliotii</i> Baker (or as <i>M. setacea</i>)	12	(Lewis, 1966). C.P.: 15 km S of Grahamstown, <i>Goldblatt</i> 2864 (MO).
	24	C.P.: Fort Hare, <i>Goldblatt</i> 455 (BOL).
<i>M. erici-rosenii</i> Fries	12	(Lewis, 1966).
<i>M. polyanthos</i> L.f.	12	C.P.: Ladismith, <i>Goldblatt</i> 661 (BOL). Oudtshoorn campsite, <i>Goldblatt</i> 2922 (MO).
<i>M. polystachya</i> (L.f.) Ker	12	C.P.: Beaufort West, (Goldblatt, 1971a). Graaff Reinet, (Goldblatt, 1971a). 10 km W of Grahamstown, <i>Goldblatt</i> , no voucher. S.W.A.: Huns Mts., <i>Tolken</i> 3985 (BOL). (Riley, 1962).
<i>M. stricta</i> Baker (as <i>M. trita</i>)	24	Tvl.: Johannesburg, <i>Goldblatt</i> , no voucher.
	36	Tvl.: Haenertsburg, <i>Goldblatt</i> , no voucher.
Sect. <i>Vieusseuxia</i>		
<i>M. algoensis</i> Goldbl.	12	C.P.: Wildehondekloof Pass, <i>Goldblatt</i> 2840 (MO).
<i>M. aristata</i> (de la Roche) Asch. & Graeb.	12	C.P.: Observatory grounds, Cape Town, <i>Goldblatt</i> 1299 (MO).
<i>M. barnardii</i> L. Bol.	12	C.P.: Shaws Pass, <i>Strauss</i> 35 (NBG).
<i>M. bellendenii</i> (Sweet) N.E.Br.	12	C.P.: Napier, (Goldblatt, 1971a).
<i>M. caeca</i> Goldbl.	12	C.P.: Dasklip Pass, <i>Goldblatt</i> 678 (BOL).
<i>M. debilis</i> Goldbl.	12	C.P.: Caledon dist., <i>Goldblatt</i> 673 (BOL).
<i>M. gigandra</i> L. Bol.	12	Ex hort., <i>Goldblatt</i> , no voucher.
<i>M. insolens</i> Goldbl.	12	C.P.: Drayton, Caledon, (Goldblatt, 1971a).
<i>M. loubseri</i> Goldbl., ined.	12	C.P.: Langebaan, <i>Loubser</i> 2228 (NBG).
<i>M. lurida</i> Ker	12	C.P.: Klein Hagelkraal, (Goldblatt, 1971a). Hermanus, <i>Goldblatt</i> 3311 (MO). Houw Hoek Pass, <i>Goldblatt</i> , no voucher.

TABLE 1. (continued)

Species	Diploid Chromosome Number	Collection Data or Reference to Previous Work
<i>M. neopavonia</i> Foster	12	C.P.: Heuningberg, <i>Goldblatt</i> 655 (BOL).
<i>M. tenuis</i> Ker	12	C.P.: Brandvlei, <i>Goldblatt</i> 587 (BOL). Steinkopf, <i>Goldblatt</i> 2777 (MO). Hills above Hermanus, <i>Goldblatt</i> 3010 (MO).
<i>M. thomasiae</i> Goldbl.	12	C.P.: Burgher's Pass, Koo, <i>Thomas s.n.</i> (BOL).
<i>M. tricuspadata</i> (L.f.) Lewis	24	C.P.: Jeffreys Bay, <i>Goldblatt</i> 2893 (MO).
	12	C.P.: Kirstenbosch hill, Cape Peninsula, <i>Goldblatt</i> , no voucher.
<i>M. tripetala</i> (L.f.) Ker	12	C.P.: Nieuwoudtville, (Goldblatt, 1971a). Ceres, <i>Goldblatt</i> 667 (BOL). Koedoes Mts., <i>Goldblatt</i> 547 (BOL).
<i>M. tulbaghensis</i> L. Bol.	24	C.P.: Gouda Common, <i>Goldblatt</i> , no voucher.
<i>M. villosa</i> Ker	24	C.P.: Tulbagh, (Goldblatt, 1971a). Riebeeck Kasteel, (Goldblatt, 1971a).
Subg. <i>GRANDIFLORA</i>		
<i>M. alticola</i> Goldbl.	12	Natal: Drakensberg, <i>Trauseld s.n.</i> (BOL).
<i>M. graminicola</i> Oberm. subsp. <i>graminicola</i>	12	Natal: Mooi River, (Goldblatt, 1971a).
<i>M. huttonii</i> (Baker) Oberm.	12	Natal: Nottingham, <i>Moll</i> 2666 (PRE).
<i>M. macrantha</i> Baker	12	Malawi: <i>Pawek</i> 6966 (K, MO).
<i>M. moggii</i> N.E.Br. subsp. <i>moggii</i>	12	Tvl.: Lochiel, (Goldblatt, 1971a).
<i>M. schimperi</i> (Hochst) Pichi-Serm	12	Malawi: Nyika, (Goldblatt, 1971a). Livingstonia dist., <i>Goldblatt</i> 15 (J).
<i>M. spathulata</i> (L.f.) Klatt subsp. <i>spathulata</i>	12	C.P.: Knysna, (Goldblatt, 1971a). O.F.S.: Harrismith, (Goldblatt, 1971a).
subsp. <i>transvaalensis</i> Goldbl.	12	Tvl.: Graskop, (Goldblatt, 1971a).
subsp. unknown	12	(Riley, 1962).

Even with the three exceptional species in which base numbers other than $x = 10$ and $x = 6$ occur, the difference between the two main groups appears remarkable and it is unlikely with about 70% of the genus known cytologically that more species will be found linking these groups, especially as most of those unknown chromosomally are specialized and closely allied to species with $x = 6$.

Species such as *M. stricta* ($2n = 24, 36$), *M. villosa*, and *M. tulbaghensis* (both $2n = 24$) are clearly polyploid and not aneuploids derived from $2n = 20$. This is clear both because the species closely related to these polyploids have diploid numbers of $2n = 12$, and equally from considerations of chromosome length where the polyploid does in fact have approximately twice the amount of chromosome material compared with plants having $2n = 12$ or $2n = 20$ (Table 2).

The occurrence of $2n = 20$ in one population (several individuals of *M. gawleri*), while a second (only 2 specimens) has $2n = 24$ is curious. This species clearly belongs to the $2n = 20$ group and the anomalous record of $2n = 24$ may

TABLE 2. Chromosome size in several species of *Moraea*.

Species	Diploid Number $2n$	Haploid Chromosome Length μ
<i>M. falcifolia</i> Klatt	20	54
<i>M. lugubris</i> (Salisb.) Goldbl.	20	49.5
<i>M. cf. viscaria</i> (L.f.) Ker	20	68
<i>M. angusta</i> (L.f.) Ker	20	56.5
<i>M. barnardii</i> L. Bol.	12	57
<i>M. tenuis</i> Ker	12	61.5
<i>M. alticola</i> Goldbl.	12	67.5
<i>M. thomasiae</i> Goldbl.	12	61
<i>M. tulbaghensis</i> L. Bol.	24	114

be due to the presence of B chromosomes. Unfortunately, due to difficulties in growing this species, no more information is available.

While most species each has a characteristic karyotype, notable variations occur within forms of *Moraea tripetala*, particularly in the size, shape, and location of the satellite. In a few other species heteroploidy has been recorded. Variations in ploidy levels occur in *M. ciliata*, *M. elliotii*, and *M. tricuspudata* all of which have both diploid and tetraploid populations, while *M. stricta* evidently has both tetraploid and hexaploid populations. Aneuploid differences occur in *M. ciliata* with most populations $n = 10$ but $n = 9$ in one population and in *M. fugax* where *M. fugax* var. *fugax* has $n = 8$ and 6 while var. *gracilis* has $n = 10$. All these examples of intraspecific variation in chromosome number require more detailed study and will undoubtedly have significance at the species level. For the purposes of interpreting subgeneric and interspecific relationships, heteroploidy is less important and may safely be disregarded, except in *M. fugax* which will be discussed further.

Because the chromosomes are quite large in *Moraea*, ranging from about 4–8 μ in the $x = 6$ group and from 2–5 μ in the $x = 10$ group with the method described here, considerable detail of the karyotype can be seen (Figs. 1–2). Relative length of chromosomes and the position of the centromeres and satellites all contribute to greater understanding of species relationships. The size and position of the satellite are particularly useful features in indicating small natural groups. Details of karyotype relating to classification are discussed in the following pages.

SUBGENERIC CLASSIFICATION

SYNOPSIS OF TREATMENT

Subg. 1. *Moraea*

$x = 10$

Plants simple to many branched. Leaves (1–)2–many. Bracts and spathes usually acute. Corm tunics pale to black, never sticky. Outer tepals reflexed, inner either erect or spreading to reflexed. Seeds small and \pm spherical-angled.

Type species: *M. vegeta* L.

Species: ca. 21

Distribution: Cape Province, from Cape Town north to the Orange River and east to Kimberley and Grahamstown.

Sect. 1. *Moraea*

Plants few to many branched. Leaves (2-)3-many. Stem erect, produced above ground.

Type species: *M. vegeta* L. Species: ca. 10

Distribution: Cape Province, from Cape Town north to the Orange River and east to Kimberley and Humansdorp.

Sect. 2. *Acaules* Baker

Plants simple or branched. Leaves several. Stems entirely subterranean.

Type species: *M. ciliata* (L.f.) Ker Species: ca. 4

Distribution: Cape Province, from Cape Town north to Namaqualand and east to Graaf Rienett and Grahamstown.

Sect. 3. *Deserticola* Goldbl.³

Plants simple or few to many branched. Leaves solitary. Stems well developed.

Type species: *M. bolusii* Baker Species: ca. 4

Distribution: Dry areas of the northwestern Cape, from the van Rhynsdorp district in the south to southern South West Africa.

Sect. 4. *Subracemosae* Baker

Plants few to many branched. Leaves 1 or 2, with leaf inserted well above ground at base of inflorescence. Stem well developed. Capsule strongly beaked.

Type species: *M. fugax* (de la Roche) Jacq. (lectotype) Species: 2

Distribution: Namaqualand to southwestern Cape.

Sect. 5. *Tubiflora* Goldbl.⁴

Plants much branched. Leaves 2-3. Flowers solitary in spathes, with a true perianth tube and inner tepals lacking.

Type species: *M. cooperi* Baker Species: 1

Distribution: Southwestern Cape.

Subg. 2. **Monocephalae** (Baker) Goldbl., stat. nov.

Monocephalae Baker, Fl. Cap. 6: 10. 1896, basionym (sect.). x = 10

Plants unbranched. Leaf solitary, terete. Stem well developed, nodes often viscous. Bracts usually obtuse. Seeds flattened, platelike.

Type species: *M. angusta* (Thunb.) Ker (lectotype) Species: 3

Distribution: Southwestern and southern Cape as far east as George.

Subg. 3. **Visciramosa** Goldbl.⁵ x = 10

Plants several to many branched, conspicuously viscous below the nodes. Produced leaves 2. Corm tunics pale to dark brown and oily on inner surfaces. Tepals spreading to reflexed. Seeds angled.

Type species: *M. bituminosa* (L.f.) Ker Species: ca. 4

³ Sect. *Deserticola* Goldbl., sect. nov. Planta simplex ad multiramosa. Folium solitarium. Caulis producta. Typus: *M. bolusii* Baker.

⁴ Sect. *Tubiflora* Goldbl., sect. nov. Planta multiramosa. Folia 2-3. Flores solitarii in spathae; tubus perianthii productus; tepala interiora absentia. Typus: *M. cooperi* Baker.

⁵ Subg. *Visciramosa* Goldbl., subg. nov. Planta multiramosa, viscosa subnodis. Folia 2. Tunicae cormi pallidi brunneae, oleosae in pagina inferiora. Tepala effusa ad reflexa. Semina angulata. Typus: *M. bituminosa* (L.f.) Ker.

Distribution: Cape Province, from Cape Town north to Namaqualand and east to Grahamstown.

Subg. 4. **Vieusseuxia** (de la Roche) Baker $x = 6$

Plants simple to many branched. Leaves usually solitary or 3–5. Stems well developed. Bracts and spathes acute. Seeds angled or with \pm spongy testa.

Type species: *M. bellendenii* (Sweet) N.E. Br. (lectotype) Species: ca. 35

Distribution: South Africa to Ethiopia.

Sect. 6. *Polyanthes* Goldbl.⁶

Plants few to many branched. Leaves 1–5, usually solitary. Inner tepals entire, well developed. Seeds angled.

Type species: *M. polystachya* (L.f.) Ker Species: ca. 10

Distribution: Ethiopia to the southwestern Cape.

Sect. 7. *Vieusseuxia*

Plants simple or few branched. Leaf solitary (rarely 2). Flowers much modified, inner tepals usually trifid or much reduced to absent. Seeds angled or with \pm spongy testa.

Type species: *M. bellendenii* (Sweet) N.E. Br. Species: ca. 25

Distribution: South Africa, Transvaal to southwestern Cape.

Subg. 5. **Grandiflora** Goldbl.⁷ $x = 6$

Plants unbranched, usually large. Produced leaf solitary. Flowers with inner tepals entire and erect. Seeds depressed, triangulate to discoid.

Type species: *M. spathulata* (L.f.) Klatt Species: ca. 16

Distribution: Ethiopia to South Africa (excluding southwestern Cape).

DISCUSSION

Chromosome number has been a major factor in establishing natural species groups and, as a result, in influencing the subgeneric classification. Consideration of cytological data together with morphology has resulted in the placing of species with $x = 10$ (9) and including *M. fugax* with $x = 10$, 8 and 6 in three subgenera: *Moraea*, *Monocephalae* and *Visciramosa*; while species with $x = 6$ were segregated in two subgenera: *Vieusseuxia* and *Grandiflora* (Fig. 3).

As thus subdivided, each subgenus is believed to constitute a natural assemblage of species with a common ancestor. The base number of $x = 10$ is regarded as ancestral in the genus and the three subgenera with this number are probably best regarded as of great age and, while themselves natural groups, have diverged from one another to such a degree that they cannot be reasonably accommodated in a single subgenus without also including the subgenera with $x = 6$.

The species with $x = 6$ are treated as comprising the two subgenera *Vieusseuxia* and *Grandiflora*. Since they are very distinct morphologically, they are, in my

⁶ Sect. *Polyanthes* Goldbl., sect. nov. Planta pauci- ad multiramosa. Folia 1–5. Tepala interiora integra, producta. Semina angulata. Typus: *M. polystachya* (L.f.) Ker.

⁷ Subg. *Grandiflora* Goldbl., subg. nov. Planta simplices. Folium solitarium. Flores generales; tepala interiora integra, erecta. Semina depressa, triangulata ad discoidea. Typus: *M. spathulata* (L.f.) Klatt.

opinion, unlikely to have evolved in a single evolutionary line from the basic stock with $x = 10$. Thus the chromosome number of $2n = 12$ is believed to have evolved independently, at least three times, in subg. *Vieusseuxia*, subg. *Grandiflora*, and *M. fugax* (subg. *Moraea*).

Subg. 1. Moraea.—This subgenus is morphologically heterogeneous and is here divided into five sections. Section *Moraea* comprises several quite unspecialized species having from 2 to many produced leaves, usually a well developed branching system (occasionally simple in depauperate specimens) and generalized flowers with entire, \pm spreading inner tepals. This type of flower is also found in the three species of sect. *Acaules* but here the plant itself is greatly modified with a reduced aerial stem—only the upper part of the leaves and the inflorescence emerge above ground level. While the axis is still branched in *M. falcifolia*, the other species of sect. *Acaules*, *M. ciliata* and *M. macronyx*, are more reduced and are unbranched.

The karyotypes of sect. *Moraea* and sect. *Acaules* are, with the exception of *M. papilionacea* ($2n = 18$), strikingly similar: there are usually 3–4 pairs (occasionally 5) of long chromosomes and a corresponding number of much smaller pairs. The satellites are usually large and located on a small chromosome pair (Figs. 1B–D). *Moraea vegeta* and *M. papilionacea* (Goldblatt, 1971a: 345–346) are exceptions with satellites on long chromosomes, and this may be indicative of a natural relationship as they are morphologically quite similar. In *M. ciliata* and *M. macronyx* there are a second pair of satellites on long chromosomes as well as the pair on short chromosomes.

The affinities of sect. *Deserticola*, unusual in subg. *Moraea* in having a solitary leaf, are clearly with species such as *M. serpentina* of sect. *Moraea* and the karyotype of *M. bolusii* (Fig. 1E) is almost identical with that of *M. serpentina* (Fig. 1D); the chromosome complement is distinctive in comprising three long, two medium long and five small chromosome pairs. The asymmetrical corm with its black, fibrous tunics of species of sect. *Deserticola* is very like those of *M. serpentina* and their relationship is very close; in fact, the presence of the single leaf was the only factor in deciding on sectional status for this small alliance.

Moraea fugax in which chromosome numbers of $n = 10$, 8, and 6 have been recorded, as well as the dubious $2n = 28$ by Sakai (1952), is placed together with the closely related *M. filicaulis* in sect. *Subracemosae* of subg. *Moraea*. The placement in this group may appear inconsistent since the base number in subg. *Moraea* is $x = 10$, while lower base numbers predominate in sect. *Subracemosae*. The decision was influenced primarily by the nature of the karyotype in *M. fugax* var. *gracilis*, which has $n = 10$; the karyotype matches exactly those found in sect. *Moraea*, and comprises six long acrocentric chromosomes and seven much shorter pairs (Fig. 1F). *Moraea fugax* var. *gracilis* appears, from the morphological point of view, ancestral to other forms of *M. fugax*, as well as *M. filicaulis*, as it is a large much branched plant in contrast with the smaller, fewer branched forms with lower chromosome numbers. In other respects it is similar to var. *fugax* and *M. filicaulis*, having in common with these the peculiar leaf insertion high up on the stem and the beaked ovary, unique to this group. A critical survey of the cytology of the heteroploid and also morphologically variable *M. fugax* seems

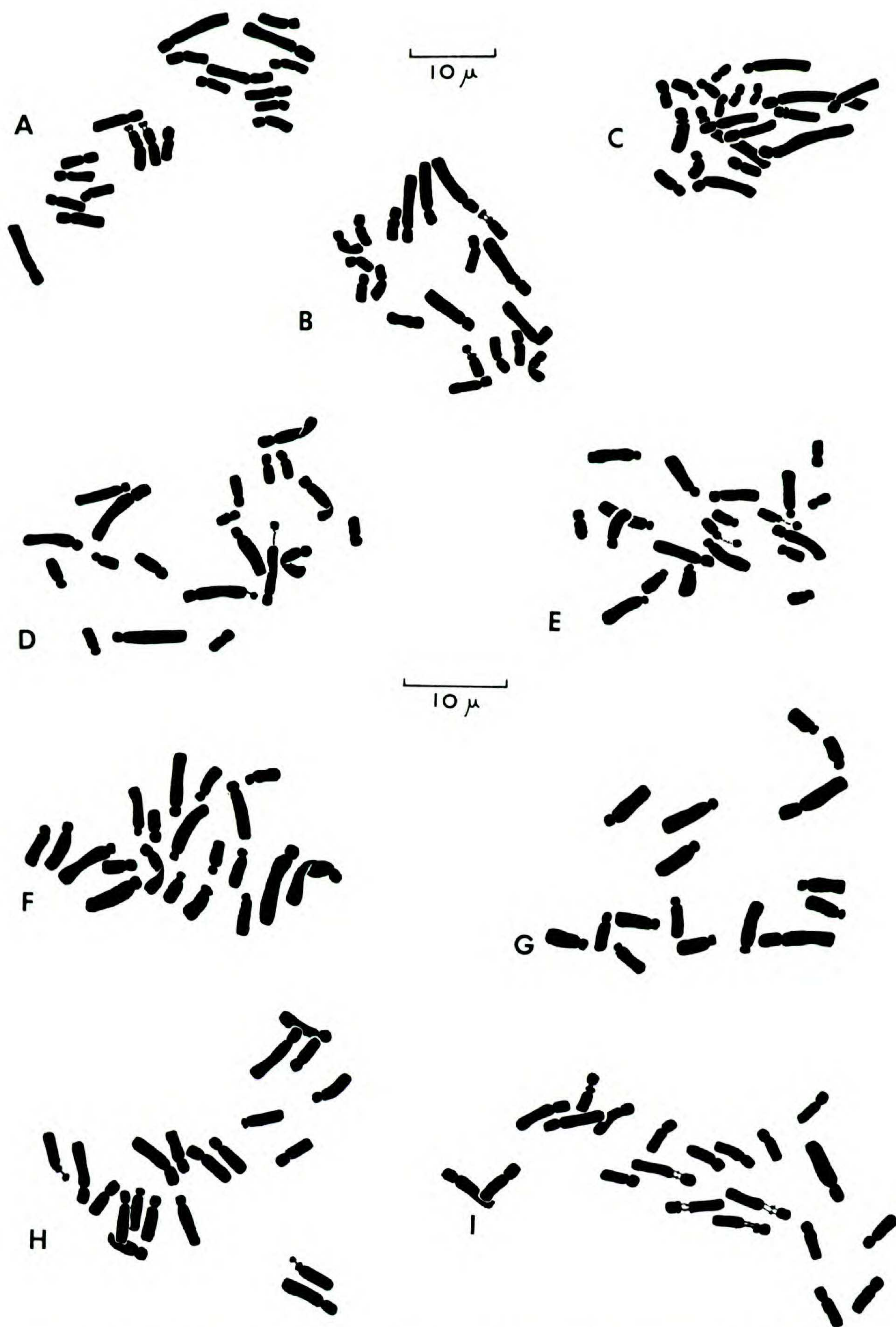


FIGURE 1. Karyotypes in *Moraea* subgenera *Moraea*, *Visciramosa*, and *Monocephalae*.—A. *M. cooperi*.—B. *M. lugubris*.—C. *M. falcifolia*.—D. *M. serpentina*.—E. *M. bolusii*.—F. *M. fugax* var. *gracilis*.—G. *M. fugax* var. *fugax*.—H. *M. angusta* (s.l.).—I. *M. elsiae*. [Upper scale applies to A-C, H-I; lower to D-G.]

called for and species limits will almost certainly be redefined in the light of further cytological and morphological study.

Section *Tubiflora*, comprising only one species, *M. cooperi*, resembles sect. *Moraea* vegetatively in having a ramified axis. Its flowers are, however, unique in the genus, having a true perianth tube; the flowers are also unusual in being solitary in each inflorescence spathe and in lacking inner tepals. Unusual as *M. cooperi* is, the karyotype is like those found in sect. *Moraea* in having long pairs and large satellites on one of the seven short pairs of chromosomes (Fig. 1A).

Subg. 2. Monocephalae.—Subgenus *Monocephalae* is small, comprising *Moraea angusta* and the two species *M. neglecta* and *M. anomala* segregated by Lewis (1949). Lewis's treatment is followed here with reservation, as the species of the section require critical morphological study. Species in subg. *Monocephalae* have a very distinctive morphology with a simple stem and a solitary terete leaf, but the flowers are unspecialized, large and usually yellow. Without cytological data, the affinities of the species in this section would have remained misunderstood, for the general morphological reduction, large generalized flowers, and the flattened seeds are strongly reminiscent of subg. *Grandiflora* and these two subgenera were in fact regarded as a single section by Baker in his treatment. Other features, such as the somewhat obtuse bracts and spathes, and the sticky exudate below the nodes in some forms suggest affinity with subg. *Visciramosa*. While the chromosome number of $2n = 20$ (Fig. 1H) places subg. *Monocephalae* close to subg. *Moraea*, the karyotypes are not particularly alike and size differences between the chromosomes are not at all distinct. The similarities of subg. *Monocephalae* to subg. *Grandiflora* are believed to be independently derived, and *M. angusta* and its two allies probably evolved in parallel fashion with subg. *Grandiflora* to achieve the reduction of branching and leaf number while retaining an ancestral chromosome number.

Subg. 3. Visciramosa.—This remarkable group stands in a somewhat isolated position. The ± 4 species, which are characterized by a highly ramified inflorescence, curiously sticky patches on the stem below each node, a distinctive corm with brown tunics covered by an oily secretion, and flowers with broad, spreading to strongly reflexed segments and occasionally free stamens, give no particular indication of relationships to other groups within the genus. The chromosomes of the three species studied are similar and the karyotype of only one species, *M. elsiae*, is illustrated (Fig. 1I). There are no sharp size differences amongst the chromosomes, though 2 to 3 larger pairs occasionally stand out; a distinguishing feature of the karyotype is the characteristically small satellite found on a small chromosome pair. This satellite location is frequent though not invariable in the $x = 10$ group.

Subg. 4. Vieusseuxia.—Although subg. *Vieusseuxia* is by far the largest subgenus with ± 35 species, about 40% of the genus, it is morphologically more uniform in vegetative habit than the $x = 10$ group, though the flower is much more varied. With the exception of *M. polystachya*, *M. polyanthos*, *M. carsonii*, its close allies, and a peculiar form of *M. tripetala*, all species have a single produced leaf and relatively few or no branches. In contrast to the vegetative uniformity, the flowers of many species have become specialized in remarkable ways.

Many natural species groups can be recognized in this subgenus but only two major groups are given recognition as sections. The least specialized species are placed in sect. *Polyanthes* with *Moraea polystachya* and its allies. They include forms with a much branched axis and 3–5 leaves, as well as more specialized forms with a solitary leaf and fewer branches. The flowers are generally unmodified and are blue. The karyotypes found in this section are perhaps the least specialized of the species with a base number of $x = 6$, in that they are usually fairly symmetrical, an unspecialized karyotypic feature.

Apart from similarities in the karyotypes of closely related species, the karyotypes found in sect. *Polyanthes* are varied and suggest that the section comprises several distantly related entities. A comparison of the karyotypes of *M. polyanthos* (Fig. 2F) with the previously published figure for *M. stricta* (as *M. trita*) (Goldblatt, 1971a: 348) illustrates this contention. Sect. *Polyanthes* is regarded as a link between subg. *Moraea* and sect. *Vieusseuxia* but chromosomal data place it firmly in the latter. In spite of its intermediate position it is not possible to give sect. *Polyanthes* higher rank as species like *M. elliotii* clearly link the group to sect. *Vieusseuxia*, exhibiting strong similarity to *M. algoensis* and *M. tripetala*, and the dividing line between the two sections is almost arbitrary.

Sect. *Vieusseuxia* is characterized by modification and reduction of the inner tepals in most species, exceptions being *Moraea insolens*, and some forms of *M. neopavonia* and *M. lurida*. Typically the inner tepals are small and trifold but many may be quite reduced to short entire cusps or are absent as in *M. barnardii*. The trend to reduction of the inner tepals is not unique and also occurs quite independently in sect. *Moraea* where some forms of *M. fergusoniae* have trifold tepals while in *M. cooperi* they are absent. The section contains several distinct groupings each with characteristic morphology and karyotype.

Moraea tripetala and its allies, such as *M. algoensis*, *M. barnardii*, *M. debilis* and *M. tenuis* (Figs. 2A, B, C), have similar karyotypes, usually with a small satellite on a long chromosome pair. Some variability occurs within species especially in *M. tenuis* and *M. tripetala* where satellites differ in size and position. The so-called peacock moraeas, *M. neopavonia*, *M. villosa*, *M. tulbaghenis*, *M. loubseri*, and *M. caeca* (Figs. 2D, E), characterized by outer tepals with a broadly ovate to circular limb, usually with a bright color and with distinct markings, have a karyotype in which one of the longest chromosome pairs is submetacentric and bears small satellites.

In contrast, *Moraea bellendenii*, *M. lurida*, *M. insolens*, and *M. tricuspida*, which appear to be closely allied, do not share many karyotypic features. Large satellites are located on long metacentric chromosomes in *M. bellendenii* and *M. insolens*, and are variable in *M. lurida*, being either large and located on a long metacentric pair or on a smaller, acrocentric pair, while in the heteroploid *M. tricuspida*, the satellites are small.

The karyotype of *Moraea thomasiae* with its acrocentric chromosome complement (Fig. 2G) is rather different from other species in sect. *Vieusseuxia*. This tends to confirm its rather isolated position in the alliance.

Several species in this section occur in the summer rainfall area of South Africa and await cytological examination.



FIGURE 2. Karyotypes in *Moraea* subgenera *Vieusseuxia* and *Grandiflora*.—A. *M. barnardii*.—B. *M. debilis*.—C. *M. tenuis*.—D. *M. caeca*.—E. *M. neopavonia*.—F. *M. polyanthos*.—G. *M. thomasiae*.—H. *M. alticola*.

Subg. 5. Grandiflora.—In marked contrast to the previous subgenus, subg. *Grandiflora* is florally uniform and all species have large, usually yellow flowers which have erect inner tepals and spreading outer tepals. Nevertheless the group is believed to be advanced and is very modified in vegetative character. The large produced leaf is always solitary and the branching is entirely reduced (only in the rarest cases are individuals of *M. huttonii*, or *M. spathulata* ever branched). Cytologically the section is very uniform and the karyotype of *M. alticola* (Fig.

2H) is representative of the group; there are two pairs of submetacentric chromosomes, the remaining four are acrocentric to almost telocentric, and a small satellite is present on a long, often apparently telocentric chromosome pair. All too few species of this widespread group are cytologically known and those from tropical Africa especially require investigation. Morphological uniformity however suggests that few cytological surprises are to be expected.

Note on Baker's Classification in Flora Capensis.—Baker's view of *Moraea* was much broader than the one accepted here, as two of his four subgenera, *Dietes* and *Helixyra*, are today regarded as distinct genera, the last mentioned now *Gynandriris*. Baker's remaining two subgenera, *Vieusseuxia* and *Moraea* (as *Eumoraea*), are retained in name only, for the composition and circumscription are entirely altered. Owing to the poorly known state of *Moraea* when Baker worked, his errors are easily understood. In some cases correction of his treatment was only possible with recourse to cytological data. As an example, Baker's *Monocephalae* can be quoted; in this section he included both *M. angusta* ($2n = 20$) and *M. spathulata* ($2n = 12$), as well as two other species not conforming even to his own definition of the section. *Monocephalae*, treated here as a subgenus, is retained in a narrow sense including only *M. angusta* and its two close allies. Wherever possible, Baker's sections are retained, though often redefined so as to conform to the revised system. Thus, when possible, the older treatment is followed or emended and the present system represents a continued refinement initiated by the author (Goldblatt, 1973) through new methods of study.

EVOLUTION

The underlying assumption throughout this paper has been that the $x = 10$ (9) group of species, i.e., subgenera *Moraea*, *Monocephalae*, and *Visciramosa*, comprise the more primitive part of the genus, a hypothesis based primarily on morphological evidence. Most species in subgenera *Moraea* and *Visciramosa* have more than one leaf and numerous branches, a condition believed to be the ancestral growth form in the genus. Though specialized species with a single leaf and with reduced branching are found in the primitive subgenera with $x = 10$, notably the species of subgenus *Monocephalae*, the great majority of the species with this reduced habit, including those with very specialized flowers, have low chromosome numbers, either 8 or predominantly $x = 6$. As indicated earlier, there is reason to believe that the low base number of $x = 6$ was derived independently in at least three lines of evolution (Fig. 3).

The cytological data strongly support the basic assumption that $x = 10$ is the base number for *Moraea*, for as already shown, diploid species with $n = 10$ have approximately the same amount of chromosome material as species with $n = 6$ and cannot therefore be derived by polyploidy and subsequent loss of chromosomes from the latter group. Thus, $x = 6$ is seen as having been derived from an ancestral base number of $x = 10$ by decreasing aneuploidy, and the author's earlier tentative suggestion to this effect (Goldblatt, 1971a: 356) is therefore maintained. One surprising feature, however, is the paucity of intermediates between $x = 10$ and $x = 6$; *Moraea papilionacea* with $n = 9$, a form of *M. ciliata* also with $n = 9$ and *M. fugax* with $n = 10, 8,$ and 6 being the only known exceptions. Sub-

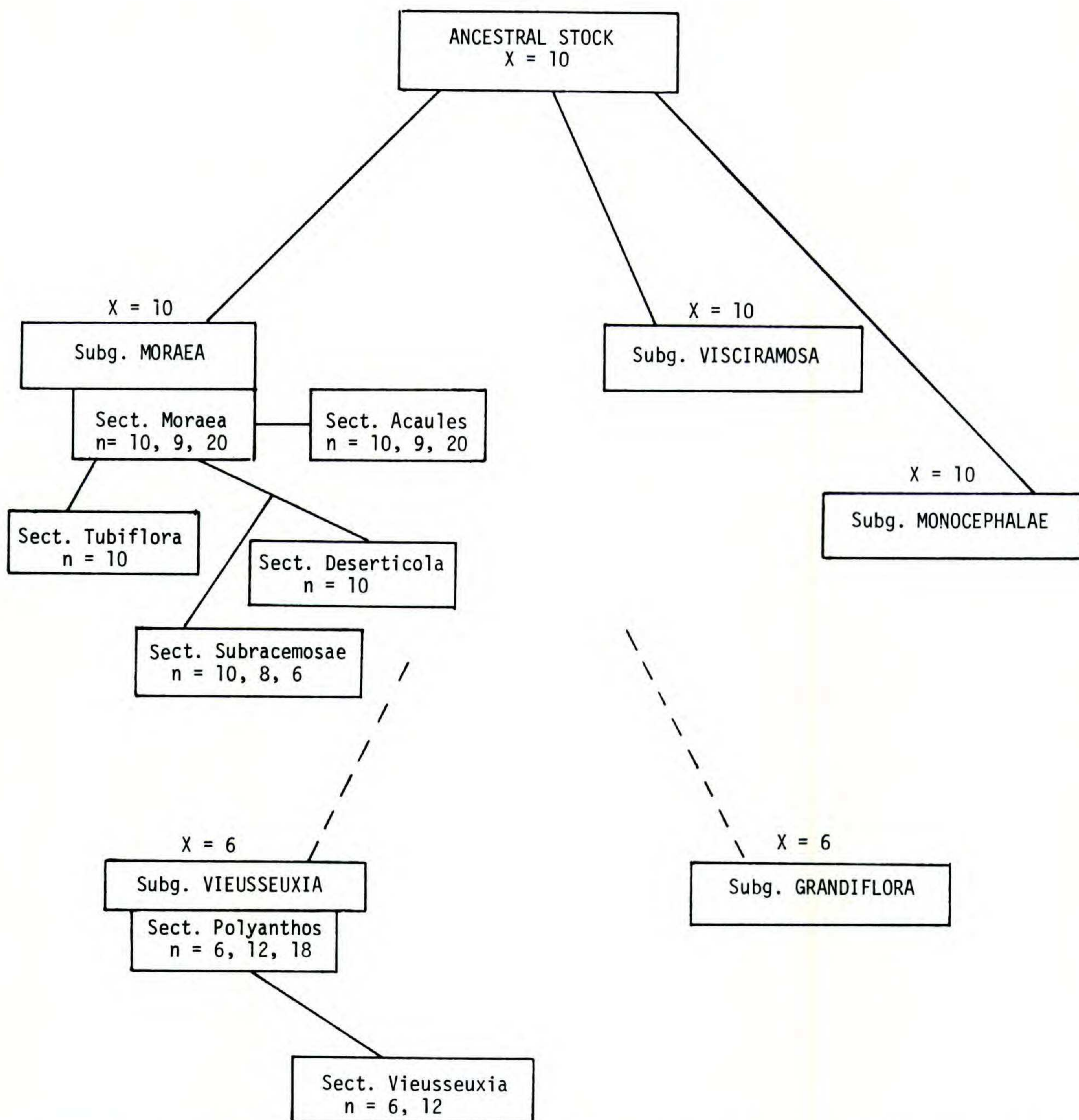


FIGURE 3. Diagrammatic representation of presumed phylogenetic relationships of subgenera and sections in *Moraea*.

genera *Vieusseuxia* and *Grandiflora*, as well as *M. fugax* and *M. filicaulis* of subg. *Moraea*, each with $x = 6$, are probably not of particularly recent origin and their independent derivation (Fig. 3) suggests that this low chromosome number has considerable selective value. Once this was achieved, rapid evolution followed. The two subgenera with $x = 6$, subg. *Grandiflora* and subg. *Vieusseuxia*, comprise by far the largest number of species with $\pm 75\%$ of the species. Though both subgenera may be of some age, a very recent spurt of evolution appears to have occurred resulting in the numerous species now found, particularly in the Mediterranean region of South Africa.

The hypothesis that $x = 10$ is the ancestral condition in *Moraea* is consistent with the previously expressed view that the immediate ancestor of *Moraea* was the genus *Dietes* ($x = 10$). *Dietes*, a small genus of five African species with one

species on Lord Howe Island, Australia, is comprised of quite large, evergreen plants, usually with a branched inflorescence, a fan of many equitant leaves, and a simple *Iris*-like flower with subequal spreading tepals, petaloid styles, and distinct crests. Major primitive features are the evergreen habit, absence of a perianth tube (as in most *Moraeas*), free stamens (joined in *Moraea*), and a large persistent rhizome.

The flower of *Moraea* is similar, except in obviously highly derived forms, although the inner tepals are usually smaller than the outer and the stamens almost always are joined in a column. The vegetative form of *Moraea* is, in contrast, much modified; the plant is deciduous, the rootstock is a corm, and the leaves are much reduced. The usual iridacaeous feature, the equitant leaf, is so reduced in *Moraea* that it is represented by the morphological equivalent of an extended leaf sheath, which is terminated by a small equitant apex (Arber, 1921; Lewis, 1954; Goldblatt, 1971a). All these features suggest that *Moraea* evolved in response to strong seasonal conditions possibly when either increasing cold or more arid climates prevailed. The underground corm would thus insure survival during unfavorable periods, while the reduction in size and branching and the nature of the leaf suggest an adaptation for rapid growth during a short growing period.

Extreme cold such as accompanied by the severe glaciations in the Northern Hemisphere and a corresponding short growing season did not prevail in Africa either during the later Tertiary when *Moraea* was probably evolving or more recently. Seasonal aridity, however, does occur today and has been part of the African climatic regime since at least mid-Tertiary in areas where *Moraea* is found. As the climate deteriorated from the Miocene onward, areas bordering the tropics must have been subjected to increasing stress as a result of both summer drought and cooler winters. Such a setting is one in which *Moraea* is believed to have evolved.

That the majority of species of *Moraea* including all those with a basic chromosome number of $x = 10$ occur today in the southwestern Cape and Namaqualand under a winter rainfall, dry summer regime, might suggest this area as the place of origin of the genus. However, the origin of the genus under such a climate seems untenable in view of the current belief that true Mediterranean type climates such as found in the southwestern Cape may not be much more than three million years old (Raven, 1973; Axelrod, 1973). *Moraea* is almost certainly considerably older and the primitive species of *Moraea* that now all occur in the Cape region may perhaps be relicts surviving only in this area owing to lack of competition. Alternatively, *Moraea* may have evolved entirely in this area under different climatic conditions.

It is, however, evident that the extraordinary radiation of *Moraea* in the Cape winter rainfall area is a direct result of the violent climatic fluctuations during the Pleistocene (e.g., Schalke, 1973) and the development of an extreme Mediterranean climate. Most of the present day Cape species are therefore probably of quite recent origin, probably less than 1–2 million years old, with the more localized species which occupy specialized habitats probably only a few tens of thousands of years old.

The center of evolution of *Moraea* is perhaps somewhere to the north of the

Cape winter rainfall zone in the interior of central Southern Africa, between latitudes 10° and 30°S which includes Namaqualand where several primitive species occur today. Parts of this region are arid semidesert while others are dry savanna, and this area is perhaps the most sensitive to climatic changes such as envisioned in the evolution of *Moraea*. Today, with the exception of the eastern mountain ranges and Namaqualand, this area is the habitat for few species of *Moraea* but contains a scattering of unrelated species. It is of interest, though, that the most primitive species of *Ferraria*⁸ (base number $x = 10$), *F. glutinosa*, the only freely branched species of this otherwise Cape genus, occurs throughout this zone. It is allied to *Moraea* and perhaps evolved from *Dietes* in much the same way as *Moraea*. It seems likely that the ancestors of the modern species of *Moraea* may also once have inhabited this region.

The occurrence of the specialized subgenera *Grandiflora* and *Vieusseuxia* in the eastern mountains of Africa as far north as Ethiopia, with subg. *Grandiflora* also in West Africa, is probably a fairly recent development. These subgenera are undoubtedly the most specialized and thus probably of comparatively recent origin, although the montane habitat may be of considerable age.

NOMENCLATRURAL NOTES AND NEW SPECIES

Although a detailed revision of the winter rainfall area species of *Moraea* is planned, and this is where most nomenclatural changes will be made, I have used what are now known to be correct specific names in this paper and several changes in current usage require explanation. The cytology of 4 undescribed species was discussed earlier in this paper and these new species are described below.

1. ***Moraea gawleri*** Spreng., Syst. Veg. 5 (Index): 462. 1828, nom. nov. pro *M. crispa* (L.f.) Ker.

M. crispa (L.f.) Ker, Curtis's Bot. Mag. tab. 754. 1804, hom. illeg., non Thunb., 1787.

Iris crispa L.f., Suppl. Pl. 98. 1781.

Moraea undulata Ker, Gen. Irid. 43. 1827, hom. illeg., non Thunb., 1787.

M. decussata Klatt, Abh. Naturf. Ges. Halle 15: 367. 1882; Erganz. 33. 1882, syn. nov.

Moraea gawleri, a new name proposed by Sprengel (1828) for the illegitimate homonym *M. crispa* (L.f.) Ker, is the correct name for the species variously known in herbaria as *M. crispa* (L.f.) Ker, *M. undulata* Ker, or *M. decussata* Klatt. The former two names are later homonyms while *M. gawleri* predates Klatt's *M. decussata* by more than 50 years.

2. ***Moraea serpentina*** Baker, Handbook Irid. 52. 1892.

Moraea framesii L. Bol., S. African Gard. 17: 418. 1927, syn. nov.

Moraea serpentina Baker is regarded as a conspecific with *M. framesii*, a common N.W. Cape and Namaqualand species. The type specimens of these two species are very alike and fit within the author's concept of *M. serpentina*.

⁸ The chromosome count for this species, made by the writer, is as yet unpublished.

3. **Moraea lugubris** (Salisb.) Goldbl., comb. nov.

Ferraria lugubris Salisb., Prod. Stirp. 42. 1796. TYPE: Cape Town, base of Devils Peak, Thunberg (UPS, lectotype).

Moraea iriopetala L.f., Suppl. Pl. 98. 1781, nom. illeg., superfl. pro *M. vegeta* L.

M. plumaria (Thunb.) Ker, König & Sims Ann. Bot. 1: 240. 1805, syn. nov.

Iris plumaria Thunb., Diss. Irid. no. 16. 1782, nom. illeg., superfl. pro *M. vegeta* L.

Moraea mira Klatt, Trans. S. African Philos. Soc. 3: 202. 1885, syn. nov.

Moraea lugubris (Salisb.) Goldbl., better known as *M. plumaria* (Thunb.) Ker has had a complex nomenclatural history. This plant was first given the name *M. iriopetala* by the younger Linnaeus, this being known from the inscription on several specimens in the Linnaean herbarium. However, the way in which *M. iriopetala* was described makes the name illegitimate, and in fact nomenclaturally a superfluous synonym for *M. vegeta* L. The younger Linnaeus actually described two varieties under *M. iriopetala*, one (presumably the typical variety) listed with the synonym *M. vegeta* L., and a second with the name *M. juncea* L. cited. Subsequently, Thunberg (1782) described *Iris plumaria*, a species clearly matching the specimens annotated *M. iriopetala* in the Linnaean Herbarium. Unfortunately Thunberg cited as synonyms not only the illegitimate name *M. iriopetala*, but also *M. vegeta* and *M. juncea*, thus invalidating *Iris plumaria*. Before Ker (1804) transferred *Iris plumaria* to *Moraea* in which genus it can be treated as a legitimate new species, Salisbury (1796) provided a new name for it, *Ferraria lugubris*. Salisbury cited *M. iriopetala* and *Iris plumaria* as synonyms but both names, being illegitimate, were correctly not used. Salisbury's *Ferraria lugubris* is clearly a synonym of Thunberg's *Iris plumaria* and the younger Linnaeus's *M. iriopetala* (as this applies to material in the Linnaean collection), and Salisbury may even have seen the Linnaean specimens so annotated. Thunberg's specimens of this species in the Thunberg Herbarium at Uppsala are chosen as lectotype.

4. **Moraea fergusoniae** L. Bol., S. African Gard. 19: 294. 1929.

Moraea fimbriata Klatt, Linnaea 34: 561. 1866, hom. illeg., non Loisel, 1822; syn. nov.

Moraea fergusoniae and *M. fimbriata* are names both in current use. Although when described, *M. fergusoniae* was believed distinct from *M. fimbriata*, this is not the case. The later name *M. fergusoniae* must however be used as *M. fimbriata* is a later homonym.

5. **Moraea vegeta** L. is the correct name of the species known for many years as *M. juncea* or as *M. tristis*. For an explanation of this change in usage see Barnard & Goldblatt (1975).

6. **Moraea filicaulis** Baker, Handbook Irid. 56. 1892.

Moraea diphylla Baker, Bull. Misc. Inform. 1906:24. 1906, syn. nov.

Moraea filicaulis is an older name for *M. diphylla* and the latter is reduced to synonymy.

7. **Moraea elsiae** Goldbl., nom. nov. pro *Homeria simulans* Baker.

Homeria simulans Baker, Fl. Cap. 6: 529. 1896. TYPE: South Africa, Cape, Kenilworth, Cape Peninsula, H. Bolus 7931 (BOL, holotype; K, MO, isotypes).

Moraea elsiae is a new name proposed here for *Homeria simulans* Baker. In spite of the floral similarity of *M. elsiae* to *Homeria*, the whole appearance of the plant with its many branches, sticky internodes, short obtuse bracts, and oily corm tunics makes it clear that the plant is correctly placed in *Moraea* subg. *Visciramosa*. The original reason for placing it in *Homeria* was the reduced style crests but this character is now recognized as occurring in several species of *Moraea* also (Goldblatt, 1971b). The species is named in honor of Miss Elsie Esterhuysen, the indefatigable Cape botanist who is endeavoring to conserve its best known locality, Kenilworth Racecourse in Cape Town. A new name was necessary as *M. simulans* Baker (= *Gyrandriris*) blocks the transfer from *Homeria*.

8. For the explanation of the usage of *Moraea stricta* Baker (for *M. trita* N.E. Br.), *M. falcifolia* Klatt (for *M. fasciculata* and *M. galaxioides*) and *M. elliotii* (for *M. macra* and *M. stewartae*) see Goldblatt (1973).

NEW SPECIES

Subg. *Moraea* sect. *Moraea*

1. ***Moraea margaretae*** Goldbl., sp. nov. TYPE: South Africa, Cape, Namaqualand, pipeline track, SW of Nababeep, *Goldblatt 628* (BOL, holotype; K, MO, PRE, S, isotypes).

Planta parva, ad 15 cm alta, ramosa. Folia producta 2–3, lineares, glabra, canaliculata an teres supra. Flores pallidi-lutei; tepala exteriora ad 3 cm longa, limbis 2 mm longis; tepala interiora erecta, lanceolata.

Plants to 15 cm high, usually 1–2 branched. Corm 5–7 mm in diameter, the tunics brown, coarsely fibrous, the inner layers entire. Leaves 2–3, linear, canaliculate, often terete and twisted near apex. Stem glabrous, branching usually from the base. Spathes herbaceous, with dark brown, acute or lacerated apices; inner spathe 3–4.5 cm long, outer 2–3 cm long. Flowers few, pale yellow; outer tepals 2–3 cm long with limb 1.5–2 cm, spreading to reflexed; inner tepals erect, spreading later, lanceolate, obtuse, to 2.0 cm. Filaments \pm 5 mm long, joined for 4 mm; anthers 4–5 mm, red. Style branches \pm 7 mm with lanceolate crests 6–10 mm long. Capsule and seeds unknown. Chromosome number $2n = 40$.

Flowering time: Late September and October.

Distribution: Coarse sandy soils in Namaqualand; more common than the record suggests.

This diminutive species is known from few collections but is nevertheless quite common in central Namaqualand, a very arid region of the Cape winter rainfall region. Its pale yellow, strongly veined flowers conform to the usual pattern for the genus, but its vegetative features, especially the characteristic branching from near the base and its 2 or 3 produced leaves, indicate a position in section *Moraea* and suggest particularly a close relationship with *M. papilionacea*. The basic chromosome number of $x = 10$ confirms its sectional position. The diploid number of $2n = 40$ for the type population (only two individuals examined) suggests this species is tetraploid. *Moraea margaretae* is named after my wife whose company and help on field trips has been invaluable.

SOUTH AFRICA. CAPE: 29.17 (Springbok):⁹ 4 km W of Steinkopf (BA), *Goldblatt* 2775 (MO). Koufontein, Steinkopf dist. (BC), *Herre s.n.* (STE 11835). Pipeline road S of NababEEP (CA), *Goldblatt* 628 (BOL, K, MO, PRE, S). 8 km E of NababEEP (CB), *Goldblatt* 3061 (NBG, MO, PRE).

30.17 (Hondeklipbaai): 8 km N of Garies (BD), *Leighton* 1129 (BOL). Brackdam, hills, *Schlechter* 11120 (BM).

Without precise locality: Namaqualand minor, *Scully* 134 (BM).

Subg. *Vieusseuxia* sect. *Vieusseuxia*

2. ***Moraea thomasiae*** Goldbl., sp. nov. TYPE: South Africa, Cape, Koo dist., Burgher's Pass, *Goldblatt* 2422 (MO, holotype; K, NBG, PRE, S, isotypes).

Planta parva, 15–20 cm alta, simplex. Cormus ad 1 cm diameter, tunicis atrobrunneis ad nigris. Folium productum solitarium, canaliculatum, glabrum, inflorescentiam excedentum. Flores lutei; tepala exteriora ad 3.5 cm longa, limbis ad 2 cm longis; tepala interiora lanceolata, ad 2 cm longa.

Plants small, slender, 15–20 cm high. Corm about 1 cm in diameter, the tunics dark brown to black. Produced leaf solitary, ± basal, linear, about 3 mm wide, glabrous, exceeding the inflorescence. Scape simple. Spathes herbaceous with brown attenuate apices; inner spathe to 6 cm long, outer about half the length of the inner. Flowers yellow; outer perianth segments with a narrow, long, erect claw, 1.5 cm long, the limb reflexed, about 2 cm long; inner segments erect, narrowly lanceolate, up to 2 cm long. Filaments about 5 mm long, free almost to the base; anthers about 6 mm long. Style branches about 1.5 cm long, bearing linear crests about 1 cm long. Capsules and seeds not known. Chromosome number $2n = 12$.

Flowering time: July to mid September.

Distribution: Clay and shale slopes, usually on a south facing slope, in the Montagu and Worcester districts.

Moraea thomasiae grows in the Worcester and Montagu districts of the south western Cape in fairly arid, semikaroid areas, where it grows characteristically on south facing shale slopes. It is a very distinct species with no close relatives. Its single leaf and slender, often unbranched stem suggests that it is best placed in sect. *Vieusseuxia*. Its simple flowers with entire inner tepals are not usual in the section, although these are known, for example, in *M. incurva*. The karyotype with $2n = 12$, supports its subgeneric placement, but the predominantly acrocentric chromosomes do not suggest a close relationship with other species in sect. *Vieusseuxia*. Its somewhat superficial similarity to the *M. angusta* complex is belied by its entirely canaliculate leaf, brown to black corm tunics, and above all, its very acute bract leaves and spathes. The difference in karyotype (*M. angusta* has $2n = 20$) makes it quite clear that *M. thomasiae* is not even remotely related to *M. angusta*. The species is named in honor of Margaret Thomas, an enthu-

⁹ Note on Citation of Specimens.—The arrangement of specimens examined, following the taxonomic treatment and discussion of each species, is based on the system currently gaining acceptance in South Africa (Edwards & Leistner, 1971). The system is based on a grid, and geographical degrees of latitude and longitude define each grid which is numbered accordingly. The one degree square grids are also designated by the name of a major town within it. Grids are divided into four quarters labelled from left to right A, B, C, or D and these quarter degree squares are again divided into four and labelled A, B, C, or D. Thus, all specimens are cited with data localizing them to one-sixteenth of a degree square.

siastic and untiring South African bulb grower and collector. The living material of the many species of Iridaceae she has provided me with is gratefully acknowledged.

SOUTH AFRICA. CAPE: 33.19 (Worcester): Hex R. Pass, near summit (BD), *Mauve & Oliver* (STE). Karoo Garden, Worcester (CD), *Bayer* 7 (NBG); *Goldblatt* 2422 (MO, NBG, PRE, K). Onse Rug Farm, Worcester dist., *Barker* 9446 (NBG).

33.20 (Montagu): Oudeberg, Montagu dist. (CA), *Acocks* 20539 (NBG, PRE). Burger's Pass, Koo dist. (DB), *Thomas s.n.* (BOL); *Mauve & Oliver* 197 (STE). Vrolikheid, McGregor dist. (DD), *Jooste* 154, 181 (both STE).

3. ***Moraea debilis*** Goldbl., sp. nov. TYPE: South Africa, Cape, clay slopes SW of Caledon, *Goldblatt* 673 (BOL, holotype; K, MO, PRE, S, isotypes).

Planta gracilis, ad 15–40 cm longa, ramosa. Cormus ad 1 cm diam., tunicis pallidis. Folium productum solitarium basale, canaliculatum, pubescentum an marginibus ciliatibus. Flores purpurei decolorentes ad malvini pallidi; tepala exteriora ad 2 cm longa; tepala interiora ad 1 cm longa, erecta, filiformia, plerumque tricuspida.

Plants slender, 15–40 cm high, usually branched. Corm \pm 1 cm in diameter, the tunics pale, finely fibrous. Leaf solitary, basal, linear, pubescent on outer surface and/or ciliate on margins, exceeding the inflorescence. Stem laxly branched, rarely simple, the bract leaves dry. Spathes herbaceous, or dry above, the apex attenuate or lacerated; inner spathe 4–5.5 cm long, outer \pm half the inner. Flowers purple, fading to a pale mauve and becoming lightly speckled; outer tepals spreading, \pm 2 cm long with a slender bearded claw and a lanceolate limb \pm 1 cm long; inner tepals \pm 1 cm long, erect, filiform, usually tricuspitate with the central cusp much exceeding the laterals. Filaments \pm 5 mm long, joined for about half the length; anthers \pm 5 mm long. Style branches \pm 8 mm long, the crests lanceolate, to 3 mm. Capsule narrowly ovoid-clavate. Seeds angled. Chromosome number $2n = 12$.

Flowering time: Late September and October.

Distribution: Clay soils in the Caledon district, southwestern Cape.

This slender, almost spindly plant with its small mauve flowers and reduced inner tepals is clearly allied to the well known and widespread *Moraea tripetala*. *M. debilis* is known from several collections, all from the Caledon district of the south western Cape, where it grows in clay soils amongst small shrubs and is typically late flowering. It is distinguished by its fine, pale corm tunics, pubescent leaf and small flowers with their threadlike, trifid to tricuspitate inner tepals. The karyotype, with a diploid number of $2n = 12$, is very characteristic of *M. tripetala* and its close allies.

SOUTH AFRICA. Cape: 34.19 (Caledon): SW of Caledon (AC), *Barnard s.n.* (BOL 30694); *Goldblatt* 673 (BOL, K, MO, PRE, S). Between Bot River and Caledon, *Mauve* 4893 (PRE). Ca. 12 km E of Caledon (BA), *Barker* 10851 (NBG).

Without precise locality: Caledon dist., *Pappe s.n.* (SAM 70709); *Leipoldt* 3562 (BOL); *Schlechter* 5527 (BOL, PRE).

4. ***Moraea caeca*** Barnard ex Goldbl., sp. nov. TYPE: South Africa, Cape, top of Dasklip Pass near Porterville, *Goldblatt* 678 (BOL, holotype; K, MO, PRE, S, isotypes).

Planta 20–40 cm alta, raro ramosa. Folium productum, solitarium, canaliculatum, inflorescentiam excedentium. Flores malvescenti; tepala exteriora ad 3 cm long, ungue canalicu-

lato, pubescenti, limbis obovatis, ca. 2 cm latis; tepala interiora tricuspidata, cuspidate centrale, 5–8 mm longa, lineare, cuspidibus lateribus 2 mm longis, obtusis.

Plants slender, 20–40 cm high. Corm \pm 1 cm in diameter, with light brown fibrous tunics. Leaf solitary, linear, glabrous, exceeding the inflorescence. Stem glabrous (occasionally pubescent), usually simple. Spathes herbaceous or dry above with brown attenuate apices; inner spathe \pm 5 cm long, outer to \pm 2.5 cm. Flowers mauve-lilac with a small yellow or black nectar guide; outer tepals spreading, \pm 2.8 cm long with an erect, channelled, pubescent claw 8–12 mm long and a broadly ovate, spreading limb, to 1.8–2.2 cm wide; inner tepals tricuspidate, channelled, the central cusp 5–8 mm long, laterals to 2 mm. Filaments 2–3 mm long, united near the base only; anthers dark, \pm 5 mm long. Style branches \pm 5 mm long, the crests acute to obtuse, to 7 mm long. Capsule clavate, to 1.5 cm. Seeds angular. Chromosome number $2n = 12$.

Flowering time: Late September and October.

Distribution: The Piketberg and Twenty Four Rivers Mountains above Porterville, and locally on the Cape Peninsula, southwestern Cape; confined to sandy soils.

Moraea caeca is an attractive late-flowering species allied to the “peacock *Moraeas*,” the usually large flowered, highly colored species with very broad, outspread outer tepals with conspicuous nectar guides. This species is smaller than others of the group and instead of the bright nectar guide of yellow circled with contrasting colors, the guide is small and dark or absent. It grows in sandstone areas and is known from three somewhat isolated areas, the Piketberg and the Twenty Four Rivers Mountains on opposite sides of the Piketberg–Porterville valley and from a single collection from the Karbonkelberg on the Cape Peninsula. The karyotype with $2n = 12$ is similar to that of *M. neopavonia* and *M. villosa* (although the latter is tetraploid) in the number of metacentric and submetacentric chromosomes and in the position of the satellite.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): Kloof on SW side of the Piketberg (DC), *Barnard s.n.* (BOL). Moutons Valei, *Marloth 11509* (PRE). Hills NW of Moutons Valei, *Pillans 7488* (BOL). Piketberg (DD), *Vlok s.n.* (NBG 58948). Beyond Piketberg on Redelinghuys road, *Barnard s.n.* (SAM 52394, BOL).

32.19 (Wuppertal): Dasklip (Cardouw) Pass above Porterville (CC), *Barker 7599* (NBG, STE); *Esterhuysen 16211* (BOL); *Goldblatt 678* (BOL, MO, K, PRE). Mountain above Porterville, *Loubser 856* (NBG).

33.19 (Worcester): Driebosch, Groot Winterhoek (AA), *Haynes 858* (STE).

34.18 (Simonstown): Karbonkelberg, Cape Peninsula (AB), *Salter 3288* (BM).

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